Species richness of Cyatheales in the upper Santo Domingo Canyon, Antioquia, Colombia

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Abstract. The Regional Protective Forest Reserve of the Canyons of the Melcocho and Santo Domingo Rivers in eastern Antioquia, Colombia, spans 26,533 ha with elevations from 706 to 2,937 m above sea level. This study addresses the limited prior research on ferns in the region by observing tree ferns and allied species (Cyatheales) between 1,967 and 2,600 m above sea level. We identified 11 species: *Alsophila erinacea* (H.Karst.) D.S.Conant, *Cyathea cnemidaria* Lehnert, *Cyathea latevagans* (Baker) Domin, *Cyathea planadae* N.C.Arens & A.R.Sm., *Cyathea pauciflora* (Kuhn) Lellinger, *Cyathea nigripes* (C. Chr.) Domin, *Cyathea squamipes* H. Karst., *Cyathea tryonorum* (Riba) Lellinger, *Cyathea vilhelmii* Domin, *Lophosoria quadripinnata* (J.F.Gmel.) C.Chr. and *Sphaeropteris quindiuensis* (H.Karst.) R.M.Tryon. All species are newly recorded from the reserve, with some records representing extensions of their known distributions. This species richness within a small altitudinal gradient highlights the reserve's importance for the conservation of tree ferns in Colombia's Central Cordillera.

Key words. Montane forests, northern Andes, tree ferns

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INTRODUCTION

The Regional Protective Forest Reserve of the Canyons of the Melcocho and Santo Domingo Rivers (MS Reserve), located in Antioquia, Colombia, is a biodiversity hotspot with high ecological, scientific, touristic, and educational value. This reserve plays a critical role in biodiversity conservation and the protection of biological corridors in the Central Cordillera of the northern Andes. Encompassing a wide range of ecological zones, from Tropical Very Humid Forest to Montane Pluvial Forest, the reserve aims to restore and preserve crucial ecosystems that support endemic and endangered species while maintaining essential environmental services (CORNARE 2016).

Despite the recognized ecological importance of tree ferns and allied species (Cyatheales), there is a significant gap in knowledge regarding their distribution in the MS Reserve. Existing database records from sources such as Herbario Nacional Colombiano COL (2024), Herbario Universidad de Antioquia HUA (2024) and SiBColombia (2024), indicate that Cyatheales records from the municipality of Carmen de Viboral, Antioquia and particularly from the reserve, are relatively low compared to the species richness observed during field surveys. This gap is partly due to historical difficulties in accessing the area, exacerbated by past violence and the presence of land mines.

The order Cyatheales is characterized by a wide range of morphological diversity without obvious defining traits; some species exhibit trunk-like stems, while others possess creeping rhizomes; the stems and blades of some species are covered only with hairs, whereas others bear scales; the sori can be either abaxial or marginal, and they may be indusiate or exindusiate; the spores are globose or tetrahedral-globose, each featuring a trilete scar; the gametophytes are green and cordate (Smith et al. 2008). Of the total diversity of American Cyatheales, the family Cyatheaceae accounts for almost 95% of all species, and from this the genus *Cyathea* J. Sm. alone accounts for almost 80% (Ramírez-Barahona et al. 2011). This genus thrives predominantly in cloud forests but is also well-represented in wet montane forests. The cloud forest environment, typically found on steep mountain slopes, offers nearly constant high humidity and ample light (Tryon 1976), and tree ferns are generally restricted to regions where minimum temperatures rarely drop below freezing and where rainfall is high and evenly distributed throughout the year (Bystriakova et al. 2011).



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The family Cyatheaceae exhibits a pantropical distribution, with a marked preference for the moist inner tropics (Lehnert 2003). Scaly tree ferns are among the most conspicuous fern groups in tropical montane forests due to their frequency and size (Lehnert 2011). However, this last characteristic often results in less common and more fragmentary collections compared to other fern groups (Janssen 2006). These species play crucial roles in maintaining ecosystem balance, conserving water resources, and contributing to the landscape's aesthetic value. They have also served as a real and potential resource for rural and urban communities in various tropical countries, owing to the traditional uses of different plant structures (Cárdenas et al. 2019). Furthermore, some species of Cyatheales hold ethno-medicinal importance; for instance, the paste of the apical soft portion of the caudex is applied to cuts and wounds to prevent microbial growth and inhibit abscess formation (Nath et al. 2019).

This research aims to document tree ferns and allied species in the upper area of MS Reserve. By filling this gap in knowledge, we aim to contribute to the understanding of species richness in the region, thereby supporting the conservation objectives of the reserve and enhancing the protection of its unique biodiversity.

STUDY AREA

The following description is based on the data presented by CORNARE (2016).

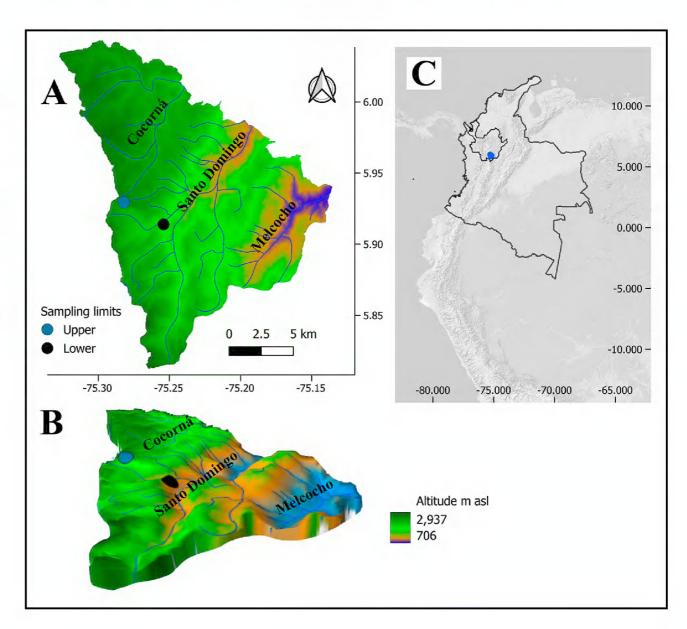
The MS Reserve is located in the municipality of Carmen de Viboral in eastern Antioquia, Colombia. The reserve spans 26,533.50 ha, with altitudes ranging from 706 to 2,937 meters above sea level (m a.s.l.). The annual average temperature ranges between 16 and 35 °C, and annual precipitation varies from 3,073 to 5,120 mm. The MS Reserve encompasses a diverse array of ecological zones, including Very Humid Forest, Lower Montane Very Humid Forest, Premontane Pluvial Forest, Premontane Very Humid Forest, Lower Montane Pluvial Forest, and Montane Pluvial Forest. Key conservation areas include water sources and aquifers, which are crucial for biodiversity preservation and ecosystem services.

The reserve hosts a diverse range of vascular plant species, with 329 species identified across 79 families within an altitudinal range of 1,200 to 2,700 m a.s.l. The forests contain large mixtures of species, with prominent families including Rubiaceae, Melastomataceae, Arecaceae, and Clusiaceae.

METHODS

To account for the heterogeneity of plant communities and the low density of some species in the study area, free-search surveys were conducted in March 2024. The surveys (Figures 1, 2) were carried out along roads and hiking trails within the altitude range of 1,967 to 2,600 m a.s.l., specifically within the area bounded by the coordinates 05°55′45″N, 075°16′55″W and 05°54′50″N, 075°15′15″W.

Figure 1. Map of Regional Protective Forest Reserve of the Canyons of the Melcocho and Santo Domingo Rivers (MS Reserve). The map highlights the sampling boundaries in relation to the overall area of the reserve. A. 2D map of the MS Reserve, depicting its three main drainages: Cocorná, Santo Domingo, and Melcocho Rivers. Upper and lower limits refer to the maximum and minimum elevations above sea level, respectively, that were sampled in this study. B. 3D reconstruction of the MS Reserve's topography. C. Location of the reserve, showing Colombia in the outer limit, Antioquia in the inner limit, and the MS Reserve marked by a blue spot.



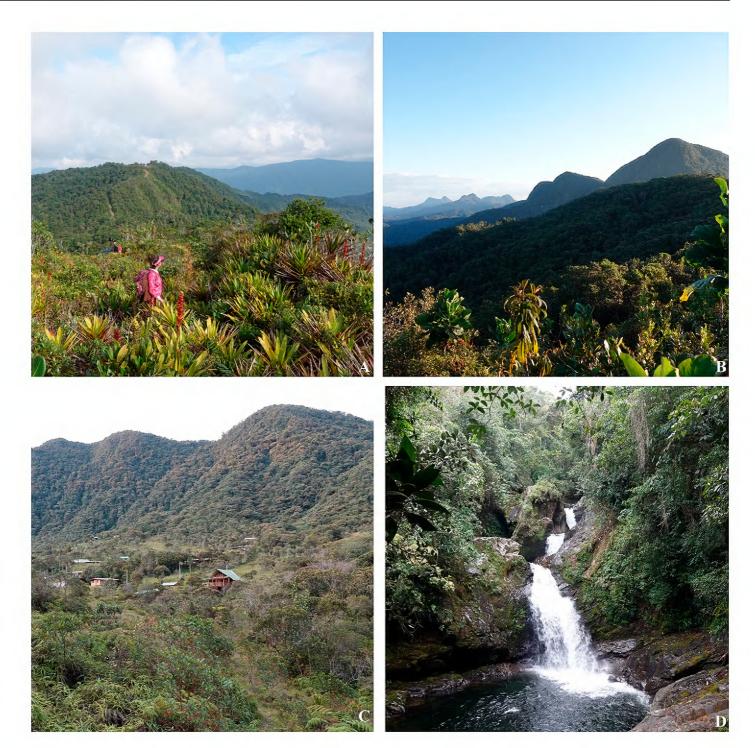


Figure 2. A. Bromeliad field in the upper sampling limit 05°55′45″N, 075°16′55″W (2,600 m a.s.l.). **B.** View of reserve, 05°55″39″N, 075°17′24″W (2,480 m a.s.l.) **C.** La Honda, 05°55′06″N, 075°16′27″W (2,149 m a.s.l.). **D.** Tributary of Santo Domingo River, 05°54′31″N, 075°15′55″W (2,030 m a.s.l.). Notice the elevation gradient and change of plant communities.

During the surveys, tree ferns were identified and georeferenced. *In situ* photographs were taken of various parts of each fern, including the entire plant, trunk apex, petiole, crozier, pinule, sori, and scales. This detailed photographic documentation was essential for accurate identification and further analysis.

The fern species were identified using established botanical keys and references (Barrington 1978; Lehnert 2006, 2008, 2009, 2011, 2012, 2014, 2016; Lehnert and Weigand 2017; Lehnert et al. 2019, 2021) Additionally, the JSTOR Global Plants (2024) online database was consulted to verify identifications and access supplementary information on the species observed.

RESULTS

We identified 11 species distributed in two families (Cyatheaceae Kaulf. and Dicksoniaceae M.R.Schomb) and four genera: *Alsophila* R.Br. with one species, *Cyathea* J. Sm. with eight species, and *Sphaeropteris* Bernh. and *Lophosoria* C. Presl with one species each. All these species are newly recorded from the MS Reserve. When a range of coordinates and elevations is provided, it indicates that multiple individuals were observed within those boundaries. A single coordinate refers to a cluster of individuals rather than a single one. For all species, no observations were made of only a single individual.

Order Cyatheales Family Cyatheaceae Kaulf.

Alsophila erinacea (H.Karst.) D.S.Conant

Figure 3A

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; between 05°54′31″N, 075°15′55″W and 05°54′50″N, 075°15′15″W; 1,967–2,030 m a.s.l.; 06.III.2024; Andrés Montoya obs.; along tributary slope. Observed and photographed, not collected.

Identification. Erect stem; trunks without old petiole bases; adventitious buds absent; laminae bipin-nate-pinnatifid; marginate scale with one or two dark apical setae protruding from the scale center; scales

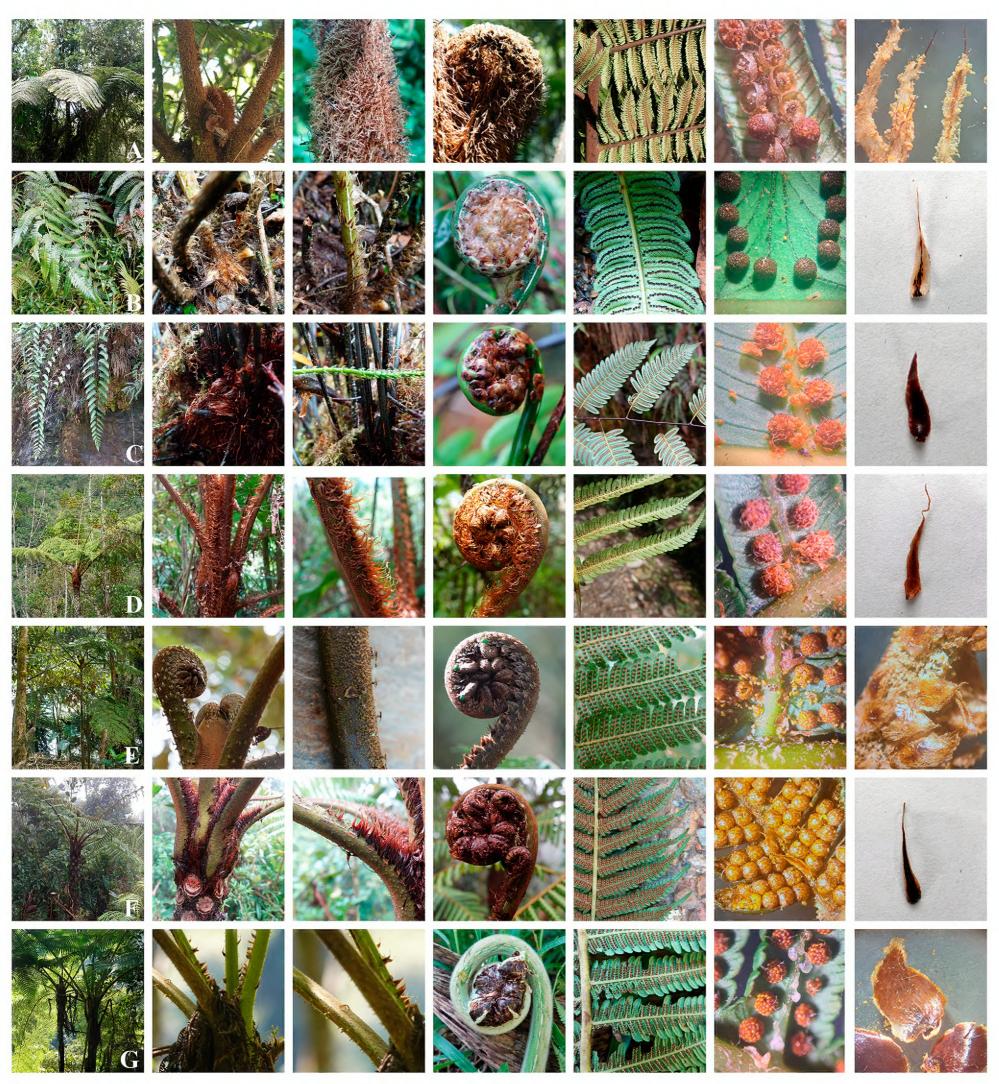


Figure 3. From left to right habit, trunk apex, petiole, crozier, pinule, sori, and scale. **A.** *Alsophila erinacea*. **B.** *Cyathea cnemidaria*. **C.** *Cyathea latevagans*. **D.** *Cyathea pauciflora*. **E.** *Cyathea planadae*. **F.** *Cyathea squamipes*. **G.** *Cyathea tryonorum*.

of the petiole with or without lateral setae; stem and petioles with black squaminate spines; squamellae with many black setae present on the lamina abaxially; indusia cyatheoid.

Cyathea cnemidaria Lehnert

Figure 3B

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; 05°55′38″N, 075°16′56″W; 2,449 m a.s.l.; 13.III.2024; Andrés Montoya obs. Observed and photographed, not collected.

Identification. Trunkless; rhizome without old petiole bases; laminae pinnate-pinnatisect, apical section comprising a small fraction of the lamina; marginate scales without apical seta; veins free, once-forked, basal ones conniving at the sinus; petiole scales sparsely scattered, concolorous whitish or bicolorous with

a narrow brown central stripe; petiole unarmed, trichomes lacking; sori in a single line, inframedial; indusia hemitelioid completely visible after sporangium dehiscence.

Cyathea latevagans (Baker) Domin

Figure 3C

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; 05°55′41″N, 075°16′39″W; 2,566 m a.s.l.; 13.III.2024; Andrés Montoya obs.; along road cuts and escarpments. Observed and photographed, not collected.

Identification Trunkless; laminae pinnate-pinnatifid; pinnae stalked; marginate scales without apical seta; petiole scales brown, concordantly bicolorous with very narrow, inconspicuous yellowish to pale brown margins; petioles inermous or sparsely verrucate, dark atropurpureous to black; rhizome short-ascending, covered with old petiole bases; petiole scurf absent; frond axes vinaceous to black on both sides; completely glabrous abaxially, hairy only adaxially on costae and distal parts of rachises; sori proximal to subproximal, in fork of veins, deep brown, indusia absent, receptacles globose sometimes supported by a small scale like those on the veins; paraphyses larger than sporangia.

Cyathea pauciflora (Kuhn) Lellinger

Figure 3D

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; 05°54′57″N, 075°16′15″W; 2,135 m a.s.l.; 20.III.2024; Andrés Montoya obs. Observed and photographed, not collected.

Identification. Erect stem; adventitious buds absent; laminae bipinnate-pinnatifid, apices gradually reduced; marginate scales without apical seta; petioles aculeate, basally with a line of narrowly elliptic lenticels; abundant scurf consisting of well-spaced, erect, reddish-brown, ovate-lanceolate squamules; scales bicolorous with light brown to yellowish margins, the colors not strongly contrasted; rhachises sparsely muricate in proximal parts, otherwise inermous; junctures of costae and rhachises not swollen; costules adaxially strongly prominent, ridged, and densely hairy with whitish to tan, antrorsely curved, multicellular hairs, abaxially weakly to strongly prominent, with many appressed, whitish to reddish brown trichomidia and many erect, whitish hairs to 1 mm long; flat, ovate to lanceolate scales to 3 mm long with fimbriate margins, and bullate squamules to 1 mm long, with elongate tips; sometimes densely scurfy like the costae; indusia absent; receptacles globose, 0.3–0.4 mm in diameter, paraphyses numerous, straight or distally contorted, whitish.

Cyathea planadae N.C. Arens & A.R. Sm.

Figure 3E

Observation. COLOMBIA – Antioquia • El Carmen de Viboral, Vereda La Honda; 05°55′15″N, 075°16′32″W; 2,185 m a.s.l.; 20.III.2024; Andrés Montoya obs. Observed and photographed, not collected.

Identification. Erect stem; trunk glabrous without old petiole bases and with lateral buds and aerial roots; the apex not hidden between petiole bases. laminae bipinnate-pinnatifid; marginate scales without apical seta; pad-like pneumathodes at the junctions of rhachises; petiole scales very scarce and fugacious, dark brown centrally; petiole scurf well developed, dark brown pulverulent; petiole with corticinate spines; sori borne at the vein fork, the indusia sphaeropteroid, fragile, evanescent, and visible only as a basal cup or cup fragments in mature sori.

Cyathea nigripes (C. Chr.) Domin

Figure 4

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; 05°54′31″N, 075°15′55″W; 2,030 m a.s.l.; 06.III.2024; Andrés Montoya obs. Observed and photographed, not collected.











Figure 4. Cyathea nigripes. Habit, trunk apex, petiole, pinule, and scale.

Identification. Erect stem; adventitious buds absent; laminae bipinnate-pinnatifid; marginate scales without apical seta; petiole scales reddish brown, shiny and elongated; rather abruptly reduced leaf apex, and a lustrous dark green lamina; dark brown to atropurpureous, aculeate petioles with whitish scurf and inermous; indusia lacking; With its overall dark appearance and overtopping trunk apices, which stand well above the last whorl of expanded fronds, it looks more like a species of the genus *Alsophila*.

Cyathea squamipes H. Karst.

Figure 3F

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; 05°55′37″N, 075°16′47″W; 2,483 m a.s.l.; 13.III.2024; Andrés Montoya obs. Observed and photographed, not collected.

Identification. Erect stem; trunks without old petiole bases when crown exposed or trunk taller than frond length, trunk apices hidden in fascicles of petioles; adventitious buds absent; laminae bipinnate-pinnatifid; apex gradually reduced; marginate scales without apical seta; petioles verrucate-muricate to aculeate; scurf persistent, consisting of crested, erect, brown to dark brown squamules; petiole scales blackish with distinct lighter margins brown to orange; costae and costules shortly hairy with antrorse multicellular hairs to 1 mm long adaxially, glabrescent abaxially, with crested brown squamule abaxially; sori costal, at vein forks; indusia sphaeropteroid, glabrous, tan and lustrous.

Cyathea tryonorum (Riba) Lellinger

Figure 3G

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; 05°54′37″N, 075°15′41″W; 2,110 m a.s.l.; 06.III.2024; Andrés Montoya obs. Observed and photographed, not collected.

Identification. Erect stem; trunks with old petiole bases; adventitious buds absent; laminae bipinnate-pinnatifid; marginate scales without apical seta; petiole scales concordantly bicolorous, dark brown centers and whitish margin with very few dark denticulations or none, except in crozier scales where the dark denticulations are always present; petioles and rhachises persistently hairy to glabrescent with scabrous surfaces, densely long-hairy when frond is unfurling; petioles spiny; sori inframedial exindusiate.

Cyathea vilhelmii Domin

Figure 5A

Observation. COLOMBIA – ANTIQUIA • El Carmen de Viboral, Vereda La Honda; 05°55′43″N, 075°16′45″W; 2,546 m a.s.l.; 06.III.2024; Andrés Montoya obs. Observed and photographed, not collected.

Identification. Erect stem; trunks without old petiole bases; adventitious buds absent; laminae bipin-nate-pinnatifid; apex gradually reduced; marginate scales without apical seta; scales with a turned up, out-ward-spreading tip; scales appressed to trunk, croziers and petiole bases, most scales with well-developed dark brown to blackish center but obscured by white margins due to imbricated layering; petiole inermous and with scales ovate-lanceolate; costae basally with elliptic pneumathodes and scarce scales; sori close to midveins, indusia hemitelioid.

Sphaeropteris quindiuensis (H.Karst.) R.M.Tryon

Figure 5B

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; 05°55′36″N, 075°16′53″W; 2,415 m a.s.l.; 06.III.2024; Andrés Montoya obs. Observed and photographed, not collected.

Identification. Erect stem; trunks with old petiole bases; adventitious buds absent.; laminae bipinnate-pinnatifid; conform elongate scale with marginal teeth, the ultimate segments are usually approximate and adnate, scale apex shows transition from retrorse to antrorse teeth; petiole scales generally whitish but variable, sometimes exhibiting castaneous tones; petioles and rhachises persistently hairy to glabrescent with scabrous surfaces, densely long-hairy when frond is unfurling; petioles lacking spines; costules bearing some to many bullate scales beneath especially on fertile segments, rarely they may be absent on sterile segments; indusium sphaeropteroid. At maturity, the apical umbo exhibits a characteristic splitting, dividing into two to a few distinct segments.

Family Dicksoniaceae M.R.Schomb.

Lophosoria quadripinnata (J.F.Gmel.) C.Chr.

Figure 5C

Observation. COLOMBIA – ANTIOQUIA • El Carmen de Viboral, Vereda La Honda; between 05°55′45″N, 075°16′55″W and 05°54′50″N, 075°15′15″W; 1,967–2,600 m a.s.l.; 06.III.2024; Andrés Montoya obs. Observed and photographed, not collected.



Figure 5. From left to right habit, trunk apex, petiole, crozier, pinule, sori, and scale. A. Cyathea vilhelmii. B. Sphaeropteris quindiuensis. C. Lophosoria quadripinnata

Identification. Trunkless; laminae 3-pinnate-pinnatisect; dense mat of brown to reddish, long trichomes; petiole unarmed; rhizome without old petiole bases; laminae densely to very sparsely pubescent beneath and often glaucous, veins free; sori, round, borne singly on the fertile veins, receptacle scarcely elevated, paraphysate, exindusiate.

DISCUSSION

Our findings provide important insights into the distribution of Cyatheaceae within a narrow altitudinal gradient in the Regional Protective Forest Reserve of the Canyons of the Melcocho and Santo Domingo Rivers. Our identification of 11 species of tree ferns, all newly recorded from the reserve, suggests that these species occupy very specific ecological niches. This concentration of diversity within a small gradient emphasizes the specialized habitat requirements of Cyatheaceae species in mountain environments. Additionally, the high species richness observed in this localized area further supports the recognition of the northern Andes as a hotspot of Neotropical fern diversity (Suissa and Sundue 2020).

The results of our study reflect the biogeographical patterns of Cyatheaceae across the Andes. Tejedor (2018) highlighted that middle elevations in the Central Andes, such as those around 1,000 m and 2,100 m a.s.l. in northern Peru, are hotspots for tree-fern species richness, with up to 24 species coexisting within narrow elevation bands. Similarly, our findings of 11 species within the 1,967–2,600 m a.s.l. range support the idea that middle elevations are centers of diversity for tree ferns.

The tree-fern richness in this study is comparable to other high-diversity sites in the Neotropics. For instance, Wiñaywayna-Intipunku in Urubamba, Cusco, Peru, at an elevation of 2,653 m a.s.l., has 12 species (Holgado-Rojas et al. 2019), though four were identified only to the genus. La Planada in Nariño, Colombia, has 11 species at elevations between 1,850 and 2,300 m a.s.l. (Arens and Sanchez 1998), which is equal to our findings. In contrast, Santiago Comaltepec in Oaxaca, Mexico, with an elevation range of 1,100–2,300 m a.s.l., has slightly fewer species, with eight (Merino et al. 2023). Cerro Murrucucú in Córdoba, Colombia, at lower elevations (100–1,000 m a.s.l.), has six species, with three identified only to the genus (Ruiz Vega 2023).

These comparisons emphasize how both elevation and latitude are crucial in shaping tree-fern richness. Middle elevations, typically ranging from 1,800 to 2,600 m a.s.l., seem to serve as diversity hotspots, likely due to optimal climatic conditions, including temperature, humidity, and precipitation, which support a wide range of ecological niches. As elevation decreases, particularly below 1,000 m a.s.l., tree-fern richness tends to decline, possibly due to warmer temperatures and lower humidity that limit species distribution. Latitude also influences these patterns, as tropical and subtropical regions closer to the equator, like Peru and Colombia, tend to support higher species richness compared to more temperate regions, where fewer species are found despite similar elevation ranges. This highlights the combined influence of both altitude and geographical position in driving tree fern diversity across the Neotropics.

All 11 species recorded in this study have been previously reported to the department of Antioquia. However, *Cyathea planadae*, *Cyathea squamipes*, *Cyathea vilhelmii*, and *Sphaeropteris quindiuensis* have

Table 1. Previous known distribution of the species registered in the present study in Antioquia, Colombia. The asterisks indicate species that have been previously documented in Antioquia, but only on the eastern slope of the Western Cordillera or further north on the western slope of the Central Cordillera and have not been recorded in the vicinity of the MS Reserve. The synonym in parentheses indicates the name used in the cited references.

	Distribution	
Species	Source: Rodríguez et al. 2013	Sources: Arango Gutierrez and Valencia Escobar 2022 Ramirez et al. 2024, SiBColombia 2024
Alsophila erinacea	Santa Rosa de Osos, Rionegro, and Sonsón plateaus, Magdalena Medio Valley, Porce River Valley. Central Cordillera, eastern slope of the Western Cordillera. 500–2,500 m a.s.l.	
Cyathea cnemidaria		
(Cnemidaria tryoniana)	Santa Rosa de Osos, Rionegro, and Sonsón plateaus. Central Cordillera. 2,000–2,500 m a.s.l.	
Cyathea latevagans	Santa Rosa de Osos, Rionegro, and Sonsón plateaus. Central Cordillera. 1,500-2,500 m a.s.l.	
Cyathea pauciflora	Santa Rosa de Osos, Rionegro, and Sonsón plateaus. Porce River Valley, Central Cordillera. 500–2,500 m a.s.l.	
Cyathea planadae*		Jericó. Eastern slope of the Western Cordillera 2,085 m a.s.l.
Cyathea nigripes	Santa Rosa de Osos, Rionegro, and Sonsón plateaus. Porce River Valley, Central Cordillera. 1,000–2,000 m a.s.l.	
Cyathea squamipes*	Campamento, Urrao. Western slope of the Central Cordillera, eastern slope of the Western Cordillera. 1,500–2,000 m a.s.l.	
Cyathea tryonorum	Santa Rosa de Osos, Rionegro, and Sonsón plateaus. Porce River Valley, Central Cordillera. 1,500–3,000 m a.s.l.	
Cyathea vilhelmii (Cyathea heliophila)*		Ciudad Bolivar. Eastern slope of the Western Cordillera 2,085 m a.s.l.
Sphaeropteris quindiuensis*	Campamento, Amalfi, Andes, Anorí, Betania, Jardín. Western slope of the Central Cordillera, eastern slope of the Western Cordillera. 1,500–3,000 m a.s.l.	
Lophosoria quadripinnata	Santa Rosa de Osos, Rionegro, and Sonsón plateaus, Porce River Valley. Central Cordillera, eastern slope of the Western Cordillera. 500–2,500 m a.s.l.Central. 1500–3500 m	

only been documented in Antioquia on the eastern slope of the Western Cordillera or further north on the western slope of the Central Cordillera (Table 1).

This study has significantly enhanced our understanding of the diversity and distribution of tree ferns and allied species in the upper Regional Protective Forest Reserve of the Canyons of the Melcocho and Santo Domingo Rivers in Antioquia, Colombia. By documenting 11 species, including new range expansions within the department of Antioquia, we have added valuable data to the limited existing records of tree ferns for this region. Our findings underscore the importance of the reserve as a critical habitat for Andean Cyatheales and highlight its role in biodiversity conservation. Further studies are needed to explore the species richness across the full altitudinal range of the reserve. This will provide a more comprehensive understanding of the diversity of ferns in this region.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist

Ethical statement

No ethical statement is reported.

Author contributions

Conceptualization: AML. Data curation: AML, ML. Formal analysis: AML, ML. Funding acquisition: AML. Investigation: AML, ML. Methodology: AML. Resources: AML, ML. Supervision: ML. Visualization: AML. Project administration: AML, ML. Software: AML. Validation: ML. Writing — original draft: AML. Writing — review and editing: ML.

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Data availability

All data that support the findings of this study are available in the main text.

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